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Original Article

Testing reproductive allometry in fish

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Energy allocation models have proved useful for clarifying the ecological mechanisms which influence growth and reproduction schemes in species with indeterminate growth and for understanding how traits correlate with generate the life history of specific species. In view of the need to understand how exploitation affects species for which few data on key population parameters such as reproductive potential and population growth rate are available, it would be helpful if simple energy allocation schemes parametrized by easily obtainable data could be used to estimate parameters such as reproductive effort and output. Testing the predictions of three such models on fecundity data from a range of species, we show how the simplifications required in a generalized energy allocation scheme are reflected in the deviations between model predictions and empirical data, and discuss the validity of the assumptions underlying these models. We caution against over-reliance on generalized and simplified models to predict reproductive effort.

Keywords: allometry, energy allocation model, fish ecology, reproductive effort.

Introduction

Reproductive output, the rate of egg or offspring production, is an important part of the relationship between parent stock size and subsequent recruitment (Lambert, 2008). For fish, this relationship is likely to depend on a number of biological processes including the production of eggs, egg fertilization and mortality, hatching, and growth and survival of larvae and prerecruits. These processes vary over time and space, are difficult to study in the field, and cannot yet be predicted with sufficient accuracy. Hence, where catch predictions or estimates of maximum sustainable yield are needed, the stock–recruitment relationship is often described by fitting fairly simple models, such as the Beverton and Holt model (Beverton and Holt, 1957) or the Ricker model (Ricker, 1954), to observations of past recruitment and spawning-stock biomass.

Increasing rates of exploitation of marine stocks have emphasized the need to identify maximum sustainable yield and other fisheries reference points for poorly studied fish populations, such as many sharks and rays (Dulvy *et al.*, 2008, 2014; Carruthers *et al.*, 2014). For these so-called data-limited or data-deficient fish stocks, where little or no information about stock size and/or recruitment is available, the parameters of the stock recruitment models cannot be estimated. Instead, it has been proposed to use life-history parameters such as the maximum size or the size at maturity of the species to predict the relative vulnerability to exploitation. This can be done by using the life-history parameters to derive estimates of the steepness of the stock–recruitment relationship at low levels of spawning stock size (e.g. Mangel *et al.*, 2010) or by using them to derive a lower limit for the spawning reproductive potential, the ratio between the egg production in the exploited and unexploited situation (e.g. Jennings *et al.*, 1998; Le Quesne and Jennings, 2012; Hordyk *et al.*, 2015).

Life-history theory suggests that small short-lived species should allocate more energy relative to size to current reproduction than large longer-lived species that are likely to spawn several times during their lifespan (Stearns, 2000). However, due to the variety of reproductive patterns found among fish, few data are often available to predict how reproductive effort, defined as the proportion of the available resources invested in reproduction, responds to the size of the species, to its longevity and to environmental variation affecting the feeding, metabolism, and mortality of the mature population (Tomkiewicz *et al.*, 2003; McBride *et al.*, 2015). Nevertheless,

estimates of total annual egg production have been found to reflect observed recruitment patterns better than spawning-stock biomass in within species comparisons (Kell *et al.*, 2015). Furthermore, comparing across species, Denney *et al.* (2002) found recruitment to be negatively related to fecundity, to age at maturity and to maximum length, but positively related to growth rate, while Rickman *et al.* (2000) found recruitment variability to be positively linked to fecundity after differences in phylogeny had been accounted for. Understanding how reproductive output and effort scale with body size or growth rate across species might therefore prove useful for evaluating the relative resilience of different fish species to exploitation.

Several models have been proposed to link the reproductive output of fish to the growth rate of the individuals, but their predictions have rarely been tested. Here we investigate the extent to which reproductive output and reproductive effort, defined as the proportion of total growth allocated to egg and offspring production, can be predicted from the von Bertalanffy growth model, which has frequently been used in both theoretical and empirical studies of fish growth. We begin by describing the von Bertalanffy model and how it can be used to predict the scaling of reproductive output with body weight at maturation. We then select three models that use the von Bertalanffy parameters to predict reproductive effort and show how their underlying assumptions affect their predictions. Finally, using data on growth and reproduction from 71 species and populations of fish including both teleosts and elasmobranchs, we evaluate the capacity of the models to reliably convert growth parameters into predictions of reproductive effort.

The von Bertalanffy growth model and reproductive effort

In species with indeterminate growth, such as most fish, the lifetime growth trajectory is often well described by von Bertalanffy's growth equation:

$$\frac{\mathrm{d}W}{\mathrm{d}t} = aW^n - bW^d, \tag{1}$$

where a, b, n, and d are constants, W is body weight, and t is age. This equation was derived by Pütter (1920) and von Bertalanffy (1938) as a mechanistic model of fish growth based on a simple mass balance argument. In the expression, aW^n represents the net rate of energy assimilation and bW^d the rate of energy loss with a the assimilation coefficient and b the loss parameter (von Bertalanffy, 1938; Ursin, 1967; Day and Taylor, 1997; Essington *et al.*, 2001). von Bertalanffy furthermore assumed that the net rate of energy assimilation would scale with body surface ($n = 2/3$), while the rate of energy loss would scale with body weight ($d = 1$). These assumptions make it possible to integrate equation (1) and arrive at a formula for body weight at age:

$$W(t) = \left(\frac{a}{b}\right)^3 \left[1 - \exp\left(-\frac{b}{3}(t - t_0)\right)\right]^3, \tag{2}$$

where t_0 is a theoretical age for which $W(t_0) = 0$. Using $W = qL^3$, where L is length, the equation can be transformed to:

$$L(t) = q^{-1/3}\frac{a}{b}\left[1 - \exp\left(-\frac{b}{3}(t - t_0)\right)\right]. \tag{3}$$

In the literature, equations (2) and (3) are usually expressed in terms of the von Bertalanffy growth parameters, $L_\infty = q^{-1/3}(a/b)$, $W_\infty = (a/b)^3$, and $k = b/3$ (Andersen *et al.*, 2008; Charnov *et al.*, 2013), where L_∞ and W_∞ are the asymptotic length and weight and k is the rate at which this size is approached. In this case, equations (1)–(3) turn into the familiar von Bertalanffy equations for growth rate, weight at age, and length at age:

$$\frac{\mathrm{d}W}{\mathrm{d}t} = 3kW_\infty^{1/3}W^{2/3} - 3kW, \tag{4}$$

$$W(t) = W_\infty[1 - \exp(-k(t - t_0))]^3, \tag{5}$$

$$L(t) = L_\infty[1 - \exp(-k(t - t_0))]. \tag{6}$$

As originally formulated, the rate of energy loss in equation (1), bW, must include costs associated with both somatic maintenance and reproduction. Assuming that the maintenance cost per cell and unit of time is fixed, the total maintenance costs should increase linearly with the number of cells and hence be proportional to W. Similarly, empirical studies have shown that reproductive output per unit of time to a first approximation is proportional to W in many fish species (e.g. Roff, 1983; Wootton, 1992, though there are exceptions). Hence, for a mature fish, the loss parameter b can be interpreted as being equal to $m + r$, where m and r are the specific loss rates due to costs associated with maintenance and reproduction. We will refer to these rates as maintenance cost and reproductive effort, respectively.

When the asymptotic size has been reached the rate of growth is zero according to equation (4). Inserting W_∞ in equation (1), this implies that $bW_\infty = aW_\infty^{2/3}$. Because fish close to their asymptotic size are rarely observed in research survey samples, for many species, in particular elasmobranchs, the within species relationship between body weight and reproductive output is difficult to establish. Analyses of reproductive allometries may be simplified by standardizing measurements to the reported size at maturation, which can be established independently of growth parameters from observed maturity ogives. Defining the relative body weight at maturation as $\eta_W = W_m/W_\infty$ and replacing the total loss parameter b with the maintenance cost and the reproductive effort $m + r$, the equality can be reformulated to:

$$(m + r)W_m = a\eta_W^{-1/3}W_m^{2/3}. \tag{7}$$

Consequently, at maturation, the expected reproductive output is $R_m = rW_m \propto a\eta_W^{-1/3}W_m^{2/3}$. However, for this proportionality to be valid in cross-species analysis neither a nor η_W must scale with the asymptotic size of the species.

Several relatively simple models yielding predictions of reproductive effort from growth parameters have been proposed (e.g. Day and Taylor, 1997; Lester *et al.*, 2004; Thygesen *et al.*, 2005; Charnov, 2008; Charnov *et al.*, 2013; Andersen and Beyer, 2015). The last four models retain the basic assumption that $R_m \propto aW_m^n$ but differ in the interpretation of how energy usage, or costs due to loss rates, change over a lifetime. By comparison, Day and Taylor (1997) consider reproductive effort r to increase with age and Lester *et al.* (2004) deviate from the growth assumption of equation (1) by assuming that the assimilation coefficient changes at some point in early life such that a differs between young and old individuals. If growth is the only available empirical measure, the assimilation coefficient a is calculated implicitly as a part of the overall energy allocation. The predicted reproductive effort r will therefore depend on the chosen cost allocation scheme. It is also worth noting that equation (6) and thus the parameters k and L_∞, which are typically obtained by excluding very young individuals, describe a

smooth asymptotic growth curve from t_0 onwards, although early life growth is often better described by an unconstrained power law of the type $dW/dt \propto W^n$ (Beyer, 1989; Day and Taylor, 1997).

We select three of the models listed above (Charnov, 2008; Charnov *et al.*, 2013; Andersen and Beyer, 2015) to examine the effect of different assumptions of energy allocation schemes on the assimilation coefficient a and the prediction of reproductive effort r. We exclude the model by Thygesen *et al.* (2005), whose assumptions are similar to those of Charnov *et al.* (2013), the Day and Taylor (1997) model, whose assumption of non-constant r differs from the main pattern in fish (Roff, 1983; Wootton, 1992), and the Lester *et al.* (2004) model, which does not calculate the assimilation coefficient.

Methods

The selected models share the assumption that reproductive output can be expressed as a fixed proportion of body size per unit time such that reproductive output at maturation can be modelled as $R_m = rW_m \propto aW_m^n$, but differ in the interpretation of the energy loss, and therefore in the calculation of the assimilation coefficient a, as described below. It should also be noted that the value of the assimilation exponent n has been the subject of some debate (e.g. Bertalanffy, 1957; West, 1997; Glazier, 1999, 2005, 2015a,b; West *et al.*, 2001), with some suggesting that the limitations of the internal circulatory system may justify a value of $n = 3/4$, rather than $n = 2/3$. The former was chosen by the authors of the third model described below. However, as discussed by Glazier (2015b) many different processes contribute to the scaling of metabolic rate with body size and the value of the overall metabolic exponent may differ between taxa, and respond to the environment of the animal, as well as to its internal state. The value of the exponent is not expected to substantially affect the fit between model predictions and data (as discussed in Glazier, 2005), although it alters the predicted reproductive investment. For consistency, we use $n = 2/3$ in our comparisons, but we also run model 3 for $n = 3/4$ and compare the results.

(i) Model 1 (Charnov *et al.*, 2013): This model assumes that juvenile growth is described by a simple power law ($dW/dt = a_1 W^n$) and uses the relation between the growth parameters in equations (1) and (5) to give $a_1 = 3kW_\infty^{1-n}$. Furthermore, growth is assumed to be determinate so that at maturation, the energy which would otherwise be devoted to further growth is given to reproduction such that $R_1 = a_1 W_m^n$ and, consequently, $r_1 = a_1 W_m^{n-1}$.

(ii) Model 2 (Charnov, 2008): This model assumes a biphasic growth scheme with maturation denoting the switching point. Juvenile growth is assumed to obey a power law $dW/dt = a_2 W^n$. Solving the differential equation assuming that size at birth, $W(t = 0)$ is close to zero and that size at maturation $W(t = t_m) = W_m$ gives $a_2 = W_m^{1-n}/(t_m(1 - n))$. Adult growth is assumed to obey equation (1), with reproductive effort $r_2 = b$ such that $W_\infty = (a_2/r_2)^{1/(1-n)}$. Combining these equations gives relative size at maturation as $\eta_W = W_m/W_\infty = (r_2 t_m(1 - n))^{1/(1-n)}$. Rearranging equation (6) shows that $\eta_L = L_m/L_\infty = 1 - \exp[-kt_m]$. Assuming that $W \propto L^3$, $\eta_W = \eta_L^3$. Reconciling these expressions gives $r_2 = -3k\eta_L/(\log(1 - \eta_L))$.

(iii) Model 3 (Andersen and Beyer, 2015): This model proposes a growth trajectory $dW/dt = a_3 W^n - mW - r_3 \psi(W/W_\infty)W$, where m and r_3 are maintenance cost and reproductive effort, respectively, and ψ is a maturity ogive describing the proportion of mature individuals of size w in a population, $\psi(W/W_\infty) = (1 + (W/(\eta_W W_\infty)) - u)^{-1}$. The exponent u specifies the width of the maturity ogive and is set to $u = 10$. The maturity ogive function is close to 0 for very small individuals ($W << W_m$) and serves to confine costs of reproduction to mature individuals. Defining a maintenance fraction parameter $\varepsilon = m/(m + r_3)$, the lifetime growth function is given by $dW/dt = a_3 W^n[1 - (W/W_\infty)^{1-n}(\varepsilon + (1 - \varepsilon)\psi(W/W_\infty))]$. The value of a_3 is taken to be that which minimizes the difference between the model predictions and the size trajectory described by equation (5). In practice, Andersen and Beyer (2015) used equation (5) to calculate weight at age at 10 regularly spaced points in time (between age 1 years and the age at which 95% of the asymptotic size is attained) and found the value of a_3 which gave the best fit, assuming a fixed value of the maintenance fraction $\varepsilon = 0.8$. Back calculating gives $r_3 = a_3(1 - \varepsilon)W_\infty^{n-1}$.

The different assumptions underlying the models result in different approaches to calculate growth and consequently the energy available for reproduction, as shown in Figure 1.

To test the accuracy of the models, we collected growth parameters and other lifehistory data from published sources on a range of fish species from which we generated model predictions as well as empirical estimates of reproductive output and effort. Reproductive output was calculated as $\hat{R}_m = F_m W_0$ and reproductive effort as $\hat{r} = \hat{R}_m/W_m$, where F_m is fecundity at maturation and W_0 is the egg or offspring weight. The species included in the analyses are determinate spawners (Murua and Saborido-Rey, 2003) and no species is reported to have more than one spawning season per year. As determinate spawners cannot generate more oocytes at a later point in the spawning season, reproductive effort for species in these dataset is limited to $r < 1$. All rates are annual. The dataset included 41 species encompassing 71 fish stocks (Supplementary material), which were treated as independent data points. All analyses were performed using R v3.2.1 software (R Core Team, 2012). The scaling analyses were performed using ordinary least square log–log regressions, $\log_{10}(Y) = \alpha + \beta \log_{10}(W_m)$, as the measurement error for W_m was assumed to be smaller than for reproductive output and growth parameters. The accuracy and bias of the models were tested by regressing the estimated reproductive output and effort on the predicted values, i.e. $\log_{10}(\hat{R}_m) \sim \log_{10}(R_m)$ and $\hat{r} \sim r$, and analysing the slope and the intercept, as advised by Piñeiro *et al.* (2008).

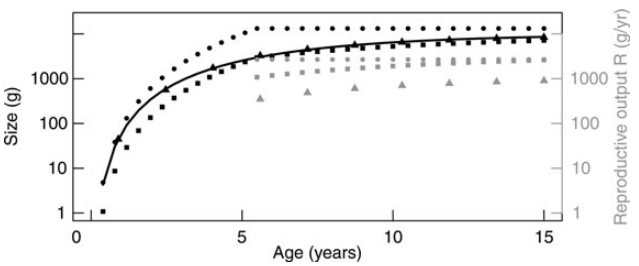

Figure 1. Predicted size (black symbols) and reproductive output (grey symbols) for a hypothetical fish with asymptotic length $L_\infty = 100$ cm, growth parameter $k = 0.1$ year^{-1}, length at maturation $L_m = 67$ cm, and length at birth $L_{t=0} = 0$ cm, for which weight $W = 0.01L^3$ g. The solid line describes growth generated from equation (6) with the above parameters; model 1 is represented by circles, model 2 by squares and model 3 by triangles.

Results

Three aspects of the predicted reproductive parameters are analysed here: the scaling of empirical estimates of reproductive output ($\hat{R}_m$) and effort ($\hat{r}$) at maturation with size at maturation (W_m) as predicted from the energy allocation schemes; the performance of model predictions compared with empirical data; and the validity of assuming independence between the assimilation coefficient a and the size at maturation.

The basis for the energy allocation models analysed here is that annual reproductive output at maturation scales with size at maturation as $\hat{R}_m \propto W_m^n$, and consequently that the reproductive effort should scale as $\hat{r} \propto W_m^{n-1}$. Figure 2a shows how $\hat{R}_m$ scales with W_m. The estimated slope $\beta = 0.84$ is significantly steeper than the assumed range of the assimilation exponent n ($2/3 \leq n \leq 3/4$); in comparison, Charnov *et al.* (2001) calculated a slope of 0.81. The size-dependency of the reproductive measures did not differ significantly between elasmobranchs and teleosts (p(slope) = 0.76, p(intercept) = 0.51). As shown by Nee *et al.* (2005), a log–log regression in which the dependent variable necessarily must be a fraction of the predictor variable (here, reproductive output at maturation depends on size at maturation as $R_m = rW_m$) tends to yield a good fit (high r^2 value) simply because the variance of the predictor variable, W_m, which spans several orders of magnitude, is much higher than the variance of the reproductive effort r, which should be in the range 0–1 for annual determinate spawners. Correspondingly, Figure 2b shows that although the scaling of reproductive effort to size is simply the slope of reproductive output −1, the scatter is much greater.

A scatterplot of observed data against model predictions should yield points clustered around a line with slope $\beta = 1$ and intercept $\alpha = 0$ (Piñeiro *et al.*, 2008). Scatterplots of reproductive output against model predictions showed the expected cluster of points with slopes quite close to 1, although Model 3 was slightly shallower (Figure 3a–c). The intercepts, however, suggest that model 1 overestimates reproduction while model 2 yields predictions on level with the empirical estimates and model 3 underestimates reproduction. Scatterplots between reproductive effort and model predictions reveal a much poorer fit (Figure 3d–f), consistent with the notion that model fit relies considerably on the size dependence of reproductive output. As suggested by Figure 3a, model 1 considerably overestimates reproductive effort and also produces several estimates of $r > 1$. Models 2 and 3 produce predictions closer to the empirical estimates, although the predictions from model 2 exceed those of model 3. Furthermore, only model 3 generates a slope that is not significantly different from unity.

The sensitivity of model 3 was examined with respect to the value of the maintenance fraction ε and the value of the assimilation exponent n. Lower values of the maintenance fraction slightly improved the fit of the predicted reproductive effort, although r^2 did not exceed 0.25, but also produced a shallower slope than the expected unity ($\beta < 1$), which would increase the risk of overestimating high values of reproductive effort. Setting $\varepsilon = 0.8$ may be considered a reasonable compromise. Running model 3 for $n = 3/4$ did not substantially affect either slope β or fit r^2 of predicted reproductive output ($\beta' = 0.92(0.035)$ vs. $\beta = 0.91(0.036)$ and $r^2 = 0.91$ vs. $r^2 = 0.9$) or effort ($\beta' = 0.89(0.21)$ vs. $\beta = 1.1(0.27)$ and $r^2 = 0.21$ vs. $r^2 = 0.19$).

An assumption underlying the use of these three energy allocation schemes is that reproductive output scales with size as $R_m \propto aW_m^n$, where the assimilation coefficient a is independent of size W_m. Examining the pattern of estimated values of a against size at maturation W_m shows that, although the relative size at maturation (η_W) is independent of W_m ($p = 0.39$, $n = 71$), this assumption is violated by all approaches towards calculating the coefficient (Figure 4). Furthermore, the estimates of model 1 are slightly higher than those of the other models, corresponding to the higher predicted reproductive output and effort generated by model 1. The difference between the predictions of models 2 and 3, however, cannot be explained by differences in the assimilation coefficient, but points to the effect of the assumed allocation of maintenance costs after maturation.

Although temperature is not specifically included in the models, it is known to affect biological rates (e.g. Gillooly *et al.*, 2001). The

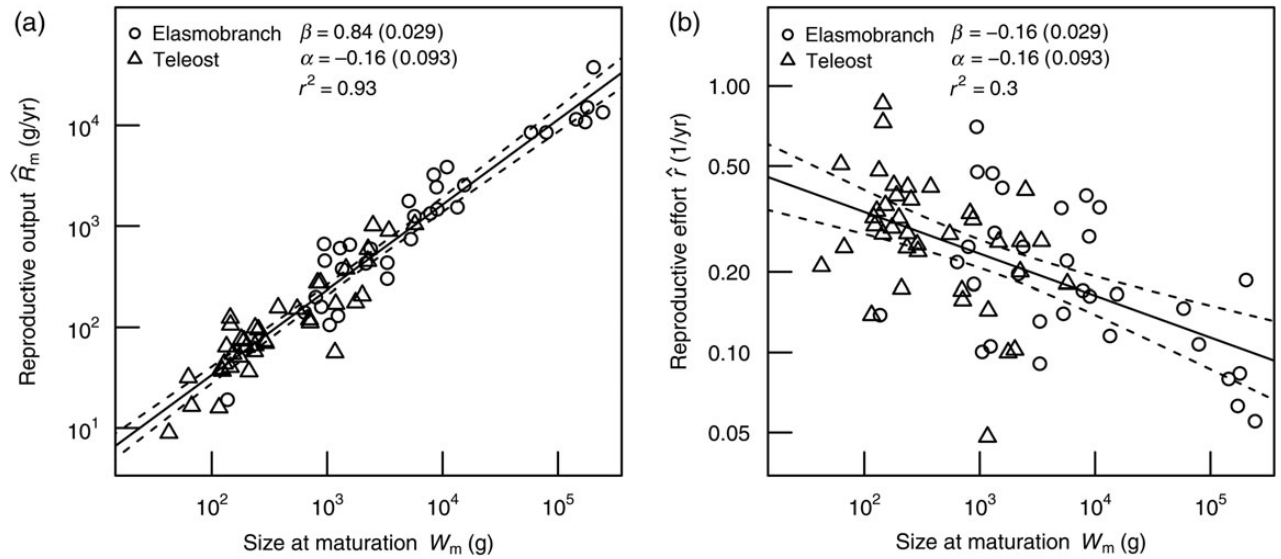

Figure 2. Relationship between (a) reproductive output at maturation $\hat{R}_m$ and (b) reproductive effort $\hat{r}$ and size at maturation W_m in 73 populations of fish. Log – log linear regression statistics shown as slope β, intercept α, and standard error in brackets; solid and dashed lines show the fitted regression with 95% confidence interval. Note that the intercept α is the logged value.

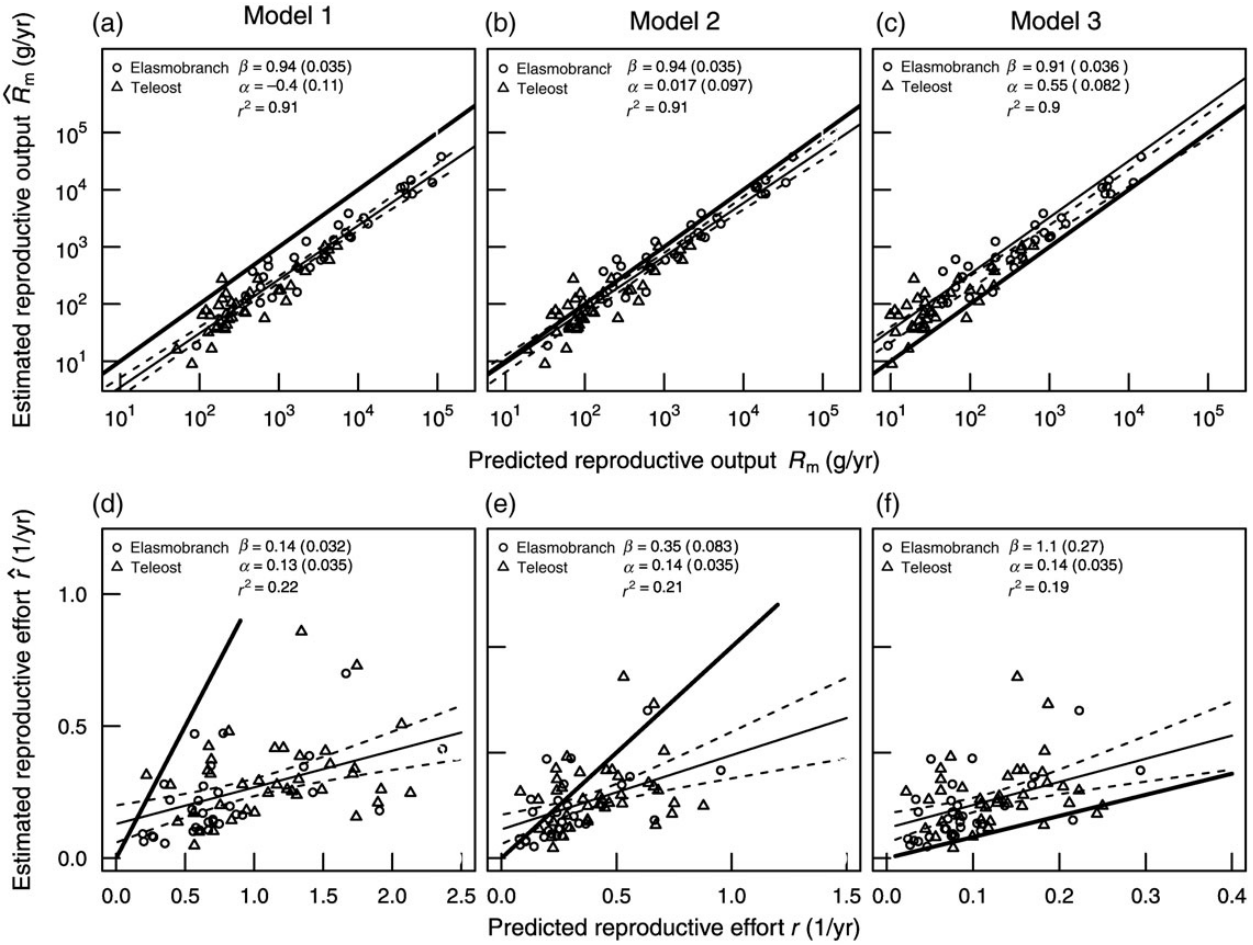

Figure 3. Relationship between estimated reproductive output $\hat{R}_m$ and model predictions (log – log linear regression; a – c) and between estimated effort $\hat{r}$ and model predictions (linear regression; d – f) in 73 populations of fish. Regression statistics shown as slope β, intercept α, and standard error in brackets; solid and dashed lines show the fitted regression with 95% confidence interval. Thicker lines indicate the 1:1 relation. Note that the intercept α in (a – c) is the logged value and that the *x*-axis differs between (d – f).

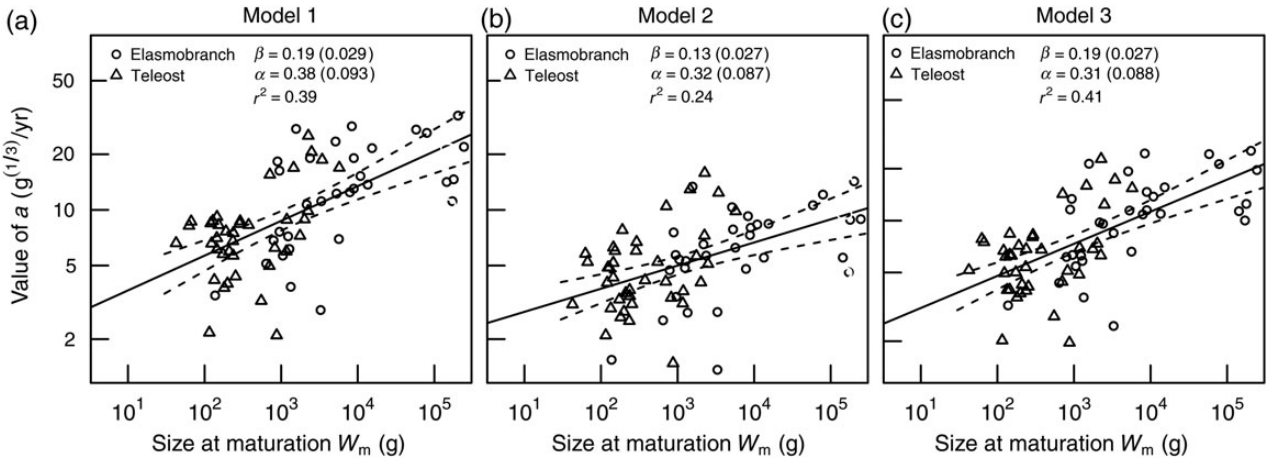

Figure 4. Relationship between size at maturation W_m and the calculated assimilation coefficient a for the three models. Solid and dashed lines show the fitted regression and 95% confidence interval. Regression statistics shown as slope β, intercept α, and standard error in brackets.

dependence on temperature was investigated by adding the inverse of the temperature in Kelvin *sensu* the Arrhenius equation as a term in the multiple linear regressions, and also by analysing the residuals of the regressions against temperature, but results were non-significant always. Regression parameters and *p*-values can be found in Supplementary material.

Discussion

Being able to predict reproductive effort and consequently fecundity, for which information tends to be scarce (Tomkiewicz *et al.*, 2003) and resource demanding to collect (Lambert, 2008), from relatively simple and easily obtained data such as growth and size at maturation could provide important information when developing management plans and assessing extinction risk of poorly studied but increasingly exploited fish stocks. For instance, Andersen and Beyer (2015) used model 3 to estimate the levels of fishing mortality that generate the maximum sustainable yield, F_{MSY}, lead to a marked decrease in recruitment, F_{lim}, or to population collapse, F_{crash}. However, as our analysis shows, models employing simple energy allocation schemes which can be parametrized using readily available growth data tend to produce predictions of limited accuracy (Figure 3d–f).

Size- and age-dependent energy allocation schemes have been used with considerable success in analyses of life histories (Kozlowski, 1991) to model the scaling of reproductive output with size (Charnov *et al.*, 2001; Andersen and Beyer, 2015). By addressing the complex three-way interaction between surplus energy, growth, and reproduction, they offer flexibility towards handling the characteristic indeterminate growth in many species of fish (Heino and Kaitala, 1999). In common with most energy allocation schemes, the models analysed here suggest that it is the surplus energy which determines reproductive effort, i.e. $r \propto aW_m^{n-1}$. However, as only growth is easily measurable, estimating the surplus energy requires assumptions on not just the assimilated energy but also auxiliary energy expenditures such as maintenance in both juveniles and adults.

Data on growth in fish are typically of the form of von Bertalanffy parameters. To predict reproduction from these parameters the von Bertalanffy model must be reinterpreted as a life-long energy budget. This is a key step as the closed-form von Bertalanffy equation describes a smooth growth trajectory throughout life, whereas an energy allocation scheme must account for the change in allocation to reproduction at the onset of maturation, and much of the difference in the predictions of the analysed models can be traced back to the method for estimating the assimilation coefficient a (illustrated in Figure 1). If the assimilation coefficient is calculated from growth and an assumed loss term, as is true when rearranging equation (1) to give equation (4), the estimated value of the assimilation coefficient is higher than it would be if no loss is assumed. Hence, model 1, which does not include a loss term when estimating the surplus energy available for reproduction, greatly overestimates reproductive effort. In model 2, the assimilation coefficient is calculated without the loss term, which lowers the estimate of the assimilation coefficient, but ignoring maintenance for all juveniles still causes growth to follow a steeper slope than equation (6) describes, as illustrated in Figure 1. Furthermore, assuming that the shift between juvenile and adult size trajectories is entirely caused by reproduction still causes model 2 to overestimate reproductive effort, although not to the same degree as model 1. Including a maintenance loss term throughout life appears to produce predictions of reproductive effort more consistent with the empirical estimates, but calculations for model 3 are slightly more cumbersome and also require an additional term, ε, which defines the ratio of maintenance loss to overall loss. It could be argued that treating ε as a species-specific parameter might improve the precision of model 3; however, Andersen and Beyer (2015) estimated the maintenance fraction ε indirectly from reproductive effort and the assimilation coefficient on the assumption that it is a species-independent parameter. As there is no independent means of calculating the maintenance fraction, this is of limited help for data-deficient stocks.

The overall applicability of energy allocation schemes for generating useful life-history predictions has been demonstrated repeatedly with single-species models (e.g. Quince *et al.*, 2008a,b; Ohnishi *et al.*, 2012). In addition to circumventing the problem of cross-species scaling of parameters, confining the analyses to a single species naturally accounts for species-characteristic aspects of reproduction. Specifically, reproductive investment is typically calculated as the proportion of body mass devoted to reproduction, R/W, while the actual cost of reproduction may include activities such as migration (Jørgensen *et al.*, 2008), courtship (Svensson *et al.*, 2004), territoriality (Dijkstra *et al.*, 2005), etc., which are likely to be specific to the habitat and the species, and therefore difficult to adequately account for outside a single-species model. Moreover, general models tend to assume a degree of constancy with respect to population growth and fecundity parameters, although these are known to vary between years and across habitats (Shelton *et al.*, 2006; Brander, 2007), possibly in response to variable habitat characteristics (Dutil and Brander, 2003; Lambert, 2008). There are few meta-analyses of the relationship between fecundity and body size in fish, and the assumption of constant reproductive effort r is typically derived from Roff (1983), although half of the 17 stocks included in that analysis showed a positive relationship between size and gonadosomatic index. By comparison, Wootton (1992) estimated the exponent between total egg volume and body length in a dataset of 238 teleost fish to be 3.09, which is slightly higher than the isometric assumption, though this too is an approximation (e.g. Bedford, 1986). Although constant or near-constant effort may be assumed to be the norm, it should not be thought of as a universal rule. However, if, as assumed by Rickman *et al.* (2000), data are more reliable for individuals close to the size at maturation, deviations from constant r should have the smallest impact if comparisons are made at W_m.

The model predictions of reproductive output and effort depend on our assumption about the lack of a cross-species scaling of the relative size at maturation (η_W) is the assimilation coefficient a with body weight at maturation. Although the empirical estimates of η_W were highly variable (mean = 0.38, standard deviation = 0.22) they did not scale with body weight at maturation. In all three models investigated, however, a did (Figure 4). This may partly be explained by a general difference between the within-species and cross-species scaling of growth parameters in fish. Sibly *et al.* (2015) analysed the von Bertalanffy growth parameters of 576 species of fish and found $\boldsymbol{k}$ to scale with $W_\infty^{-0.35}$ within species, but with $W_\infty^{-0.23}$ across species. If we use the across-species scaling of $\boldsymbol{k}$, then we would expect $a = 3kW_\infty^{1/3}$ (equations 1 and 5) to scale with W_∞ raised to a power of $0.33-0.23 = 0.10$ across species, a scaling which is not significantly different from the value estimated by model 2 (see Figure 4) and entirely consistent with the steeper than expected scaling of reproductive output with species size in Figure 2.

The data presented here suggest that the key challenge in predicting reproductive output lies with the incorporation of costs, both in terms of their timing and magnitude, and failure to provide a reasonable framework is likely to produce unrealistic predictions. Of the models tested here, model 3 which assumed a gradual escalation of the costs of reproduction mimicking the proportion of mature individuals in a population, produced the most reasonable results. Although this model is computationally more complicated and

does not provide an analytical means of calculating the assimilation coefficient *a*, the improved performance strongly suggests that maintenance costs, even if such costs would be difficult to quantify, cannot be ignored. Nevertheless, the model failed to improve the accuracy of the predicted reproductive effort, suggesting that other factors play an important part. For instance, it may be too simplistic to assume that reproductive effort translates directly to fecundity and perhaps the inclusion of qualitative factors, such as the prevalence of spawning migrations, could help improve predictions. Although energy allocation schemes are powerful tools for understanding life histories in a number of populations, extrapolation of results to data deficient species should be done with considerable attention to the underlying assumptions of these models and the particular characteristics of the species in question.

Supplementary data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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